

## RESEARCH NOTE

### SEXUAL DIFFERENCES IN METABOLIC RATES OF SPIDERS

In general, spiders are considered to exhibit resting metabolic rates about half of those measured for other poikilothermic animals of equal mass (e.g., Anderson 1970; Greenstone & Bennett 1980; Anderson & Prestwich 1982; Anderson 1987; Paul et al. 1989; Anderson 1996). However, these metabolic rates were all compared to Hemmingsen's poikilotherm mass-scaling equation (1960), which has recently been shown to systematically overestimate metabolism in small animals (Lighton & Fielden 1995). Thus, almost any data on standard metabolic rates result in low values of metabolic rate compared to this equation. More directly, Lighton & Fielden (1995) further showed that metabolic rates for spiders (22 genera) do not differ from those of ants [Formicidae (10 genera)] and beetles [Tenebrionidae (8 genera)] of comparable size. However, under prolonged starvation spider metabolic rates may be below the standard metabolic rate (Itô 1964; Nakamura 1972; Anderson 1974), thus making them well adapted to environments with unpredictable food availability.

Almost all studies on spider metabolic rates have used only adult females (Table 1). This may be due mainly to the very influential paper on the field by Anderson (1970). He reasoned that using juveniles or males may complicate the data because the growth of the juveniles or the relatively high activity patterns of males may affect oxygen consumption. However, given the many differences in life-history characteristics between female and male spiders in general (e.g., size, longevity, reproductive efforts), it might be possible that there are also ecologically significant differences in energy consumption between females and males. Indeed, Edgar (1971) reported differences in female and male growth efficiency (ratio food consumed/weight increase) in *Paradosa lugubris* (Walkenaer); and Bromhall (1987), having found a significant difference in heart-rates between males and females of

*Argyroneta aquatica* (Clerck), suggested that the sexes may have different energetic capacities. Furthermore, if females are in the reproductive state and producing eggs, it may well be that the data collected from them is not less complicated than data from juveniles or males.

In this study my aim was to compare the available data on spider metabolism from literature and present data comparing the resting CO<sub>2</sub> production rate of females and males in the wolf spider *Hygrolycosa rubrofasciata* (Ohlert 1865) (Lycosidae).

*Hygrolycosa rubrofasciata* were collected from a bog at Sattanen, northern Finland, immediately after snow melt but before the mating activities began in late May 1996. Throughout the study spiders were housed in individual plastic jars in which food and water were available continuously. Because spiders were not fasting the levels of resting CO<sub>2</sub> production may be overestimates, but this may not affect the comparison between males and females.

CO<sub>2</sub> production rates were measured with a flow-through respirometry utilizing CO<sub>2</sub> analyzer model LI-6251 connected to Sable Systems data acquisition and analysis software Datacan V (Sable Systems, Salt Lake City, Utah). Spiders were inserted into a cylinder-shaped test chamber (length 50 mm, diameter 13 mm) plugged at both ends with a rubber plug. From the incoming air CO<sub>2</sub> and moisture were removed by filtering the air through soda lime and silica gel before it went into the test chamber. From the test chamber the air with CO<sub>2</sub> produced by the spider flowed through another moisture absorbing silica gel filter to the CO<sub>2</sub> analyzer. The air flow was 150 ml per minute and it did not seem to disturb spiders. All the measurements were made at the temperature of 25 °C.

The CO<sub>2</sub> production of resting spiders was measured several times during different days. I analyzed only those measurements that were

Table 1.—Number of spider species studied. Only studies measuring directly the CO<sub>2</sub> production or O<sub>2</sub> consumption were included; studies on heart-rates were excluded sine there is no clear-cut relationship between heart-rate and metabolic rate in spiders (see e.g., Carrel & Heathcote 1976; Greenstone & Bennett 1980; Anderson & Prestwich 1982; Carrel 1987). Altogether I could find 31 studies examining 83 species belonging to 57 genera and to 19 families.

	Number of species
Female only	69
Male only	0
Both sexes	8
Sex not reported	6
Total	83

taken after the spider had been motionless for at least 5 min. Each valid measure was a mean CO<sub>2</sub> production over a period of 2–5 min. The number of measurements per spider ranged from 1 to 9 and the total time measurements lasted ranged from 2–44 min. In the analysis I used a mean value from all of the valid measurements. Between the measurements the test chamber was washed with water and dried with soft cellulose paper.

In addition to CO<sub>2</sub> production I measured the wet mass of the individuals. After finishing the metabolic rate measurements also dry mass was measured separately for the prosoma and opisthosoma.

I found a significant difference in female and male resting CO<sub>2</sub> production rates: females had 47% higher resting CO<sub>2</sub> production rate per mass unit than males (Table 2). However, the regression slopes of CO<sub>2</sub> production per mass unit and body mass did not differ between females and males ( $t = 0.01$ ,  $df = 33$ ,  $P = 0.9$ ). Similarly, neither of the slopes was significantly different from zero-slope

(females:  $t = 0.28$ ,  $df = 5$ ,  $P > 0.7$ ; males:  $t = 1.73$ ,  $df = 28$ ,  $P = 0.095$ ).

In this data set female and male wet body mass did not differ (Table 2). However, even though there was a strong and significant correlation between the wet and dry body mass in both sexes (female: Pearson's  $r = 0.87$ ,  $n = 7$ ,  $P = 0.011$ ; male: Pearson's  $r = 0.91$ ,  $n = 28$ ,  $P << 0.001$ ), females had a significantly higher dry body mass than males (Table 2). The difference between the sexes was even more pronounced when calculated for the ratio dry mass/wet mass (two sample  $t$ -test:  $t = 11.05$ ,  $df = 33$ ,  $P << 0.001$ ). Females had also higher opisthosoma/prosoma dry mass ratio than males (two sample  $t$ -test:  $t = 4.73$ ,  $df = 6.9$ ,  $P = 0.002$ ).

My results demonstrate that there are differences in resting CO<sub>2</sub> production rates between the sexes in the wolf spider *H. rubrofasciata*. The difference between sexes in resting metabolic rates is also supported by the only study so far measuring adult male spiders in any extent (Watson & Lighton 1994). They found that in *Linyphia litigiosa* (Keyserling) (Linyphiidae) male resting metabolic rate is 161% of female resting metabolic rate. Also, in *Pardosa astrigera* (L. Koch) (Lycosidae) males seemed to have higher metabolic rates than females, but no statistical analysis were presented (Tanaka & Itô 1982). In my study male resting CO<sub>2</sub> production rate was only 63% of female resting CO<sub>2</sub> production rate. One possible explanation is that females may have been in a different reproductive state: there is likely to be a significant difference in female metabolic rate during reproductive season and between reproductive seasons. One other explanation for the difference may be that in Watson & Lighton's (1994) study the male resting metabolic rate was measured within few days after copulation (i.e., after males were involved in sex-

Table 2.—Means and standard errors for CO<sub>2</sub> production (ml g<sup>-1</sup> h<sup>-1</sup>), wet body mass (mg) and dry body mass (mg) separately for males and females. Test statistics come from two-sample  $t$ -tests between males and females.

	Males	Females	$t$	$df$	$P$
Sample size	30	7			
CO <sub>2</sub> production ± SE	0.221 ± 0.007	0.325 ± 0.016	6.33	35	<<0.001
Body mass wet ± SE	21.15 ± 0.70	19.86 ± 0.67	1.05	19.6	>0.3
Body mass dry ± SE	3.80 ± 0.15	5.07 ± 0.26	3.97	33	<0.001

ual activities), while in my study males were not allowed to copulate prior to measurements. Copulation might affect male activity levels. In any case differences between sexes in metabolic rates of spiders can not be generalized with the results from the very few studies available.

Female *H. rubrofasciata* had higher dry mass/wet mass ratio, and higher dry opisthosoma mass/dry prosoma mass ratio than males. The latter ratio is easily explained by the morphological difference between female and male abdomens: females have larger abdomens than males. The former ratio, however, is more complicated. It suggests that females have higher dry matter content per wet mass unit than males.

Organisms are mostly composed of lipids and proteins. Lipids generally contain approximately 20% water while proteins contain approximately 80% water. Thus, the difference in the dry mass/wet mass ratio indicates that females and males contain different ratios of these materials. Since females use lipids in egg production, it is not surprising to find such a difference in dry mass/wet mass ratios between sexes. These results are consistent with the study by Carrel (1990) examining the water content in the wolf spider *Lycosa ceratiola* Gertsch & Wallace. He reported a similar difference in dry mass between the sexes and came to the same conclusion that—because of the egg production—females may contain more lipids and thus less water than males.

In spiders there seem to be differences between sexes in heart-rate (Bromhall 1987), growth efficiency (Edgar 1971) and metabolic rate (Tanaka & Itô 1982; Watson & Lighton 1994; this study; but see Humphreys 1977 for no difference). In fact, most metabolic rate studies where both female and male spiders were studied, have found differences between the sexes. However, available literature has concentrated solely on female spiders (Table 1). Therefore, before extrapolating from the results of metabolic rates of one sex to comprehend the whole species or larger taxonomic groups, one should carefully consider the possible differences between sexes. Studying more closely these differences between sexes could give us some insight to the often so different life history strategies of female and male spiders.

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## LITERATURE CITED

- Anderson, J.F. 1970. Metabolic rates of spiders. *Comp. Biochem. Physiol.*, 33:51–72.
- Anderson, J.F. 1974. Responses to starvation in the spiders *Lycosa lenta* Hentz and *Filistata hibernalis* (Hentz). *Ecology*, 55:576–585.
- Anderson, J.F. 1987. Morphology and allometry of the purse-web of *Sphodros abboti* (Araneae, Atypidae): Respiratory and energetic considerations. *J. Arachnol.*, 15:141–150.
- Anderson, J.F. 1994. Comparative energetics of comb-footed spiders (Araneae: Theridiidae). *Comp. Biochem. Physiol.*, 109A:181–189.
- Anderson, J.F. 1996. Metabolic rates of resting salticid and thomisid spiders. *J. Arachnol.*, 24:129–134.
- Anderson, J.F. & K.N. Prestwich. 1982. Respiratory gas exchange in spiders. *Physiol. Zool.*, 55: 72–90.
- Anderson, J.F. & K.N. Prestwich. 1985. The physiology of exercise at and above maximal aerobic capacity in a theraphosid (tarantula) spider, *Brachypelma smithi* (F.O. Pickard-Cambridge). *J. Comp. Physiol. B*, 155:529–539.
- Bromhall, C. 1987. Spider heart-rates and locomotion. *J. Comp. Physiol. B*, 157:451–460.
- Carrel, J.E. 1987. Heart rate and physiological ecology. Pp. 95–110. *In* *Ecophysiology of spiders*. (W. Nentwig, ed.). Springer-Verlag. New York.
- Carrel, J.E. 1990. Water and hemolymph content in the wolf spider *Lycosa ceratiola* (Araneae, Lycosidae). *J. Arachnol.*, 18:35–40.
- Carrel, J.E. & R.D. Heathcote. 1976. Heart rate in spiders: Influence of body size and foraging energetics. *Science*, 193:148–150.
- Edgar, W.D. 1971. Aspects of the ecological energetics of the wolf spider *Pardosa (Lycosa) lugubris* (Walkenaer). *Oecologia*, 7:136–154.
- Ford, M.J. 1977a. Energy costs of the predation strategy of the web-spinning spider *Lepthyphantes zimmermanni* Bertkau (Linyphiidae). *Oecologia*, 28:341–349.
- Ford, M.J. 1977b. Metabolic costs of the predation strategy of the spider *Pardosa amentata* (Clerk) (Lycosidae). *Oecologia*, 28:333–340.

- Greenstone, M.H. & A.F. Bennett. 1980. Foraging strategy and metabolic rate in spiders. *Ecology*, 61:1255–1259.
- Hadley, N.F., G.A. Ahearn & F.G. Howarth. 1981. Water and metabolic relations of cave-adapted and epigeal lycosid spiders in Hawaii. *J. Arachnol.*, 9:215–222.
- Hemmingsen, A.M. 1960. Energy metabolism as related to body size and respiratory surfaces, and its evolution. *Rep. Steno Mem. Hosp. (Copenhagen)*, 9:1–110.
- Humphreys, W.F. 1975. The respiration of *Geolycosa godeffroyi* (Araneae: Lycosidae) under conditions of constant and cyclic temperature. *Physiol. Zool.*, 48:269–281.
- Humphreys, W.F. 1977. Respiration studies on *Geolycosa godeffroyi* (Araneae: Lycosidae) and their relationship to field estimates of metabolic heat loss. *Comp. Biochem. Physiol.*, 57A:255–263.
- Itô, Y. 1964. Preliminary studies on the respiratory energy loss of a spider, *Lycosa pseudoannulata*. *Res. Pop. Ecol.*, 6:13–21.
- Lighton, J.R.B. & L.J. Fielden. 1995. Mass scaling of standard metabolism in ticks: a valid case of low metabolic rates in sit-and-wait strategists. *Physiol. Zool.*, 68:43–62.
- Lighton, J.R.B. & R.G. Gillespie. 1989. The energetics of mimicry: the cost of pedestrian transport in a formicidae ant and its mimic, a clubionid spider. *Physiol. Entomol.*, 14:173–177.
- Maya, M., S. Jaganathan & S.A. Karuppaswamy. 1981. Respiratory mechanism of the spider, *Hippasa pantherina* (Family: Lycosidae). *Proc. Indian Acad. Sci. (Anim. Sci.)*, 90:539–543.
- McQueen, D.J. 1980. Active respiration rates for the burrowing wolf spider *Geolycosa domifex* (Hancock). *Canadian J. Zool.*, 58:1066–1074.
- McQueen, D.J., L.K. Pannell & C.L. McLay. 1983. Respiration rates for the intertidal spider *Desis marina* (Hector). *New Zealand J. Zool.*, 10:383–400.
- Miyashita, K. 1969. Effects of locomotory activity, temperature and hunger on the respiratory rate of *Lycosa T-insignita* Boes. et Str. (Araneae: Lycosidae). *Appl. Entomol. Zool.*, 4:105–113.
- Myrcha, A. & B. Stejgwilllo-Laudanska. 1970. Resting metabolism of *Araneus quadratus* (Clerc) females. *Bull. L'Acad. Polonaise des Sci., Sér. Sci. Biol.*, C1. II, 18:257–259.
- Myrcha, A. & B. Stejgwilllo-Laudanska. 1973. Changes in the metabolic rate of starved Lycosidae spiders. *Bull. L'Acad. Polonaise des Sci., Sér. Sci. Biol. C1. II*, 21:209–213.
- Nakamura, K. 1972. The ingestion in wolf spiders. II. The expression of hunger and amount of ingestion in relation to spider's hunger. *Res. Pop. Ecol.*, 14:82–96.
- Paul, R., T. Fincke & B. Linzen. 1987. Respiration in the tarantula *Eurypelma californicum*: evidence for diffusion lungs. *J. Comp. Physiol. B*, 157:209–217.
- Paul, R., T. Fincke & B. Linzen. 1989. Book lung function in arachnids. *J. Comp. Physiol. B*, 159:409–418.
- Peakall, D.B. & P.N. Witt. 1976. The energy budget of an orb-web building spider. *Comp. Biochem. Physiol.*, 54A:187–190.
- Prestwich, K.N. 1983. The roles of aerobic and anaerobic metabolism in active spiders. *Physiol. Zool.*, 56:122–132.
- Tanaka, K. & Y. Itô. 1982. Decrease in respiratory rate in a wolf spider, *Pardosa astrigera* (L. Koch), under starvation. *Res. Pop. Ecol.*, 24:360–374.
- Watson, P.J. & J.R.B. Lighton. 1994. Sexual selection and the energetics of copulatory courtship in the Sierra dome spider, *Linyphia litigiosa*. *Anim. Behav.*, 48:615–626.

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